

# Leopold von Buch's legacy: Treating species as dynamic natural entities, or why geography matters

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**Abstract:** Although not unknown in the 19<sup>th</sup> century, but underutilized in its modern sense, the idea of using reproductive isolation (or its converse, the potential to interbreed) as a criterion to define species and to distinguish species taxa from one another goes back to the German naturalist, geologist and palaeontologist Christian Leopold Freiherr von Buch [1774-1853]. As a “Darwinian before Darwin” he perceived reproductive isolation as the defining property of species and adopted for the first time (1) the non-essentialistic concept that species are not types but populations consisting of individuals or groups of such populations and (2) a model of geographic speciation. During the 19<sup>th</sup> century, which was dominated by essentialism, creationism, and a typological species concept, few naturalists grasped the importance of this concept, among them the malacologist Albert Mousson [1805-1890]. Primarily as a consequence of Ernst Mayr's synthetic works of 1942 and 1963 reproductive isolation became widely accepted as being the most valuable concept for defining biological species and the notions of geographical variation, separation, and the non-applicability of the degree of (phenotypic) distinctness became part of the biological species concept. The last two decades have seen an active phase of debate about how to define and delineate species. Emphasizing the often neglected but instructive historical perspective, the present paper briefly reviews developments leading to the wide application of the Biological Species Concept (BSC) during the mid 20<sup>th</sup> century, and contrasts and discusses this concept within the context of malacology. Although the BSC has been challenged conceptually and operationally on the basis of being non-universal, non-dimensional (i.e. horizontal only), and operationally impractical, it is argued here that alternative suggestions—such as the Evolutionary Species Concept (ESC) and especially the recently much-favored Phylogenetic Species Concept(s) (PSC)—are arbitrary (with nebulous and vague definitions), artificial and reductionistic (non-biological) and operation-oriented (serving only diagnosability), as was the 19<sup>th</sup> century typological approach, which resulted in a ballooning of species numbers. It is discussed why diagnosability is not a sufficient criterion for a species definition and argued that the PSC describes species taxa rather than defining a species concept. Outlining the species concept debate and based on this important distinction of species concepts (defining species) versus species taxa (describing species), it is concluded that the difficulties of applying the BSC are not sufficient to justify its rejection in favor of other, logically and biologically inferior concepts. Accordingly, the BSC should be favored over the PSC(s) because it is the only definition that provides an objective criterion, reproductive isolation, and is primarily based on the biological significance of species. In addition, for the demarcation of species taxa, morphological, molecular, geographic, ecological, and behavioral information should be inferred in order to rank geographically isolated populations as species or subspecies. In this context, two case studies from malacology, that utilize freshwater gastropods of the former “melaniid species basket” (Paludomidae and Pleuroceridae) are used to advocate the conception of species as representing dynamic entities in a historical and geographic context.

**Key words:** Species concepts, species taxon, biological species, phylogenetic species, typology, freshwater gastropods, Paludomidae, Pleuroceridae

“When I use a word,” Humpty replied, in a scornful tone, “it means just what I choose it to mean—nothing more nor less.” “The question is,” said Alice, “whether you can make a word mean so many different things.” “The question is,” said Humpty, “who is to be master, that's all.” (Carroll 1865).

Species are of paramount importance for biology. The species is not only the fundamental concept for systematists and the basic unit for ecology, species is also a basic unit of

the real world, and thus an evolutionary and dynamic entity, providing the units of diversity and “the coin of evolutionary change” (Mayr 1988a, 1991, 1997: 134), even for those authors criticizing various aspects of the modern synthetic theory of evolution (e.g. Gould 2002). The frequent observation that the fauna of a given region is not a chaotic assemblage of intergrading individuals of all kinds lends support to the conviction of the existence of non-arbitrary discontinuities in nature to be called species. Only with this assumption taken as a fact do the many researches into the

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details and mechanisms of the speciation process become meaningful. In addition, for any assessment of the world's biological diversity (for a recent malacological example see Bouchet *et al.* 2002), a sound judgment on what to consider a species is a *conditio sine qua non*.

It has been ignored for centuries that in contrast to other natural sciences such as chemistry and physics, biology is not striving in the same way to detect natural laws. While theories in the physical sciences are usually based on laws, those in biology are based on concepts. Biology, as all life sciences, attempts to find concepts that explain the natural world. Arguing for biology as an autonomous science and against the common attitude which favors discoveries and experiments over concepts, it is Mayr (1997: 26) who pointed out that today concepts such as evolution, natural selection, sexual selection, competition, altruism, or the gene "are as significant in biology as laws and discoveries are in the physical sciences and yet their importance was strangely ignored until quite recently." This is not saying, of course, that the discovery of new facts and observations are irrelevant, but rather that the major contributor to a new theory in life sciences is the development of new concepts. Changes in concepts (e.g. natural selection as an agent of evolution) had and still have much more impact in biology than new discoveries, as is best illustrated by the two so-called "Darwinian revolutions" (see Mayr 1991). As much as a scientific theory is not to pronounce a truth but to generate hypotheses to be tested, a concept tries to synthesize all the facts and evidence available at a given time (see also Murphy 2002).

Species as a concept is one of the most debated issues of evolutionary biology and phylogenetic systematics. With a plethora of species concepts and definitions proposed and disputes evoked, few questions in science have elicited such a long-standing and heated debate as the "species problem" (for example Dobzhansky 1935, 1937, Mayr 1942, 1957, 1963, 1988a, 1988b, 1991, 1996, 1997, 2001, Simpson 1961, Hull 1965, Peters 1970, Gittenberger 1972, Griffiths 1974, Mishler and Donoghue 1982, Cracraft 1983, 1989, 2000, Sudhaus 1984, Reif 1984, Vrba 1985, Willmann 1985, 1991, Haffer 1986, 1991, 1992, 1995b, 1998, Iwatsuki *et al.* 1986, Häuser 1987, Mishler and Brandon 1987, De Queiroz and Donoghue 1988, McKittrick and Zink 1988, Otte and Endler 1989, Frost and Hillis 1990, Nixon and Wheeler 1990, Sluys 1991, Haffer 1992, O'Hara 1993, 1994, De Queiroz 1995, Claridge *et al.* 1997, Ghiselin 1997, Eck 1998, Howard and Berlocher 1998, Wilson 1999, Wheeler and Meier 2000, Hey 2001a, 2001b, Schilthuizen 2001, see also book reviews by Avise 2000b, Hull 2002, Shaw 2002, Wake 2002). What seems to be just a semantic battle for some is the central ontological problem of systematic biology for others. In the views of some taxonomists at least, there is "already too much literature" on this problem and "it has been dis-

cussed, argued over, and symposiumed to death for years" (Winston 1999: 43). In addition, it has been claimed several times by various authors, either in arrogance or ignorance that they have found the final solution to the species problem (e.g. Ghiselin 1975, Vrba and Wheeler 1992). However, because species concepts are mostly explicitly linked to mechanisms of speciation (e.g. Chandler and Gromko 1989), discussing these concepts has profound implications for evolutionary theory and, thus, are more than just an off-side battle over words.

Since the early 19<sup>th</sup> century, at hardly any period has there been agreement over the species question or on a single accepted definition of what constitutes a species. Although for about half a century the Biological Species Concept (BSC) was widely accepted in theory and practice, with the cladistic view increasingly dominating systematic biology during the last two decades, many realized an urgent need to re-evaluate relevant and related concepts in this context. It is neither possible nor intended in the present paper to cover this ongoing debate comprehensively. Given that species are so important for evolutionary biology, systematic phylogeny, classification, and taxonomy, and that the pros and cons of the debate have not always found adequate consideration in malacological literature, though, a very brief *tour d'horizon* is attempted here with some examples from freshwater gastropods added as illustrations.

Although suggested by the title of his epic work "On the Origin of Species," it was not Charles Darwin (1859) who taught us first about the nature of species. Naturalists such as George-Louis LeClerc, Comte de Buffon [1707-1788], and Johann Friedrich Blumenbach [1752-1840], during the century before Darwin had already a fairly good perception of species based on isolation. However, their concept was based on typology, assuming the infinite existence of fixed species boundaries and a constant type (see Lenoir 1980, 1981, Ghiselin 1969, Mayr 1982, Rheinberger 1990, J. Haffer pers. comm.). Thus, the idea of reproductive isolation, or its converse, the potential to interbreed, as criterion for species discrimination was not unknown, but underutilized in our modern sense during the 19<sup>th</sup> century and the first half of the 20<sup>th</sup> century. Its modern perception in the context elaborated below goes back to the German naturalist, geologist, and palaeontologist Christian Leopold Freiherr von Buch [1774-1853]. In his accounts on the natural history of the Canary Islands, Buch (1819, 1825) perceived the criterion of reproductive isolation as the defining property of species. If one follows the century-long debate of the species problem, one gets the impression that it has been little appreciated how strongly natural processes such as the formation of species are constrained by the necessity of having to take place in a three-dimensional space. Therefore, following



Buch's original insight, I will emphasize here why geography matters as a key factor in the context of the species debate.

### TYOLOGY IN MALACOLOGY

Typological thinking, or essentialism, has long dominated systematic biology and particularly taxonomy, including paleontology (Mayr 1957, 1963, 1982, 1988a, 1997, Hull 1965, Griffiths 1974, Willmann 1985, McOuat 2001, Haffer 1997a, 1997c). For the typologist, the type (the unchanging *eidos*, here not to be confused with the type as instrument of taxonomic procedure regulated by nomenclature) is real and the variation an illusion. In contrast, for modern evolutionary biologists used to thinking about populations, the type is an abstraction (a mere statistical average or arbitrarily chosen specimen for taxonomic purpose) and only the variation is real. The typological species concept forced naturalists to consider as species different variants within a population and to recognize as full species those local populations that differed by one diagnostic character from other populations. Consequently, because this concept was entirely consistent with the belief in creationism, typology precluded any belief in descent with modification of the Darwin-Wallace theory of evolution, which replaced the idea of *eidos* from Plato's philosophy with variable populations in nature. In contrast, the typological approach to nature corresponded to morphologically delineated species in quite the same way as the recent revived focus on diagnosability does within the framework of the phylogenetic species concept (see below). For a detailed introduction on the history of typology see Mayr (1982, 1988a, 1991, 1997), and Haffer (1997c). For its role in palaeontology see Willmann (1985) and Reif (1997).

In malacology, a typological tendency prevailed for centuries. For a long period malacology was essentially not much more than "conchology," the description and naming of shells, instead of a biological discipline. This is not to deny the valuable contributions in describing nature's diversity by distinguished practitioners during what has been called the "Golden Age" of malacology (see Lindberg 2002). However, typological thinking led to focussing on the often wordy but hardly practicable descriptions of minor conchological differences of single or few individual shells instead of the characteristic features and biological properties of larger series from populations in their geographical and/or ecological context. Such thinking dominated the malacological literature not only for most of the 19<sup>th</sup> century, but continued into more recent times.

As a consequence, this restriction to conventional typology long hampered modern approaches in malacology. This stands in contrast to ornithology, for example, where proponents of the "New Systematics" transformed the dis-

cipline into a fully biological science that was then instrumental in the development of a synthesis in evolutionary theory developed during the first half of the 20<sup>th</sup> century (reviewed in Mayr 1982, Reif *et al.* 2000). With the full employment of the Darwin-Wallace theory of evolution and the study of geographical variation (the "geographical principle," as exemplified in Glaubrecht 2002), naturalists realised that (1) types (or essences) do not exist in the living world, and that (2) species are composed of populations that vary from location to location and whose individuals vary within a given population. Prior to this realization, the typological method applied in malacology led to the descriptions of a plethora of new taxa, especially species and genera, resulting in today's unmanageable taxonomic-nomenclatorial cornucopia that is illustrated in the extensive synonymies. Among the many examples, see the synonymy and taxonomy of *Littorina* Férussac, 1822 in Reid (1996) or those of some of the diverse taxa within the so-called freshwater "melaniids" (Brot 1874, Starmühlner 1976, Köhler and Glaubrecht 2001, 2002) that long prevented any meaningful phylogenetic and/or biogeographic analysis.

For this reason it would be good practice for any modern taxonomic and systematic account on molluscs to start with an evaluation of whether the specific taxa dealt with actually represent biological entities independent of human perception or instead are mere phantoms of this perception. However, most authors have for a long time worked without paying much attention to the theory of species concepts and to practical implications, more so in malacology than in other, theoretically more advanced disciplines, such as ornithology. This led to the two general trends still pertinent to systematics not only of molluscs: Either (1) assigning species names and status even to populations characterized by trivial conchological characters, insignificant morphological features, and/or low genetic differentiation or (2) merging taxa into a single species or, above the species level, into species complexes and rarely superspecies (as advocated here and explained below). These trends are exemplified in studies on limnic gastropods, for example by Hubendick (1951), Davis (1981), Ponder *et al.* (1994), and Wilke *et al.* (2000) for hydrobiid snails, by Glaubrecht (1993, 1996) for the Mediterranean cerithioidean genus *Melanopsis*, and for SE Asian taxa of the pachychilid genus *Brotia* H. Adams, 1866 *sensu lato* by Köhler and Glaubrecht (2001, 2002, 2003). This unresolved situation is certainly not rendered less complicated by the application of various molecular genetic techniques, as is revealed in studies of different evolutionary lineages, for example, among Hawaiian tree snails of the Achatinellinae (Thacker and Hadfield 2000), North American freshwater Pleuroceridae (Holznagel and Lydeard 2000), or limnic bivalves such as *Potamilius* Rafinesque, 1818 (Roe and Lydeard 1998), *Fusconaia* Simpson, 1900, *Obovaria* Rafinesque, 1819,

and *Quincuncina* Ortmann, 1922 (Lydeard *et al.* 2000), and *Corbicula* Megerle von Mühlfeld, 1811 (Pfenninger *et al.* 2002).

The arbitrariness of the widely used approach of trying to keep distinguishable populations taxonomically apart even when based on insufficient morphological characters is illustrated by the case of the freshwater pulmonate genus *Physa*. Recent findings of Dillon *et al.* (2002) considerably helped to free the confused systematics and taxonomy of American Physidae with their currently recognized c. 40 "species," many of which reveal variable and overlapping morphologies, from taxonomical (i.e. nomenclatorial) baggage. The authors were unable to detect evidence of reproductive isolation among six populations from North America and Europe of *Physa heterostroph*a (Say, 1817), *Physa integra* (Haldemann, 1841), and *Physa acuta* Draparnaud, 1805, which, therefore, should be combined under the latter species name. In another example, Falniowski and Wilke (2001) reported for (partly allopatric) populations of the two named European species *Marstoniopsis scholtzi* (A. Schmidt, 1856) and *Marstoniopsis insubrica* (Küster, 1853) extremely low genetic divergence and a lack of morphological differentiation, suggesting that all populations belong to only one species, *M. insubrica*.

On the other hand, several endemic radiations of hydrobiid snails (where the problem of species discrimination are compounded because of the scarcity of complex or quantitative characters), have been studied in the last decade for Australian taxa from artesian springs in western Queensland (Ponder and Clark 1990), from artesian springs in northern South Australia (Ponder *et al.* 1989), from Tasmania and eastern Victoria (Ponder *et al.* 1993, Ponder *et al.* 1994), as well as from springsnails in arid regions in south-western North America (Hershler and Sada 1987, Hershler and Landye 1988, Hershler 1989). In all of these cases, the authors named many previously undescribed taxa as distinct species.

Because one of the problems with the species question, in my opinion, is that we constantly lose the ground that was already conquered by others, the present paper will approach this debate from a historical perspective. We forget about the achievements of earlier authors, their ideas, approaches, and concepts that are manifest in part of the literature often erroneously regarded anachronistic, leading to the impression that each generation of biologists "re-invents the wheel" instead of modifying earlier usage. Therefore, the following account gives an overview of some of the more important disparate concepts and definitions of what species are and discusses criteria for choosing a particular species concept. Certainly by not more than a curious coincidence, my own research on limnic gastropods focuses on the same questions and phenomena Leopold von Buch pointed out so early on. Thus, adding to the historical and theoretical aspects, I will present some of the findings on freshwater

Cerithioidea and expand on the debate by introducing additional aspects to illustrate how to deal with multidimensional species from an evolutionary biologist's perspective.

## LEOPOLD VON BUCH'S SPECIES CONCEPT

In early April 1815 the Prussian geologist and naturalist Leopold Freiherr von Buch started an eight-months' journey to the Canary Islands, located off the coast of northern Africa (for a biography see Günther 1900). It was his plan to study the natural history of this archipelago. Although a geologist by profession and, thus, interested in the vulcanism of the islands, Buch's other special interest was botany. During 1815 he studied the endemic and the non-endemic plants and the vegetational differences on the various islands in the Canaries. Two years after this journey, in November 1817, Leopold von Buch gave a lecture at the Prussian Academy of Sciences in Berlin, reporting on the flora of the Canaries and discussing the relations of the vegetation of this archipelago with that of the African mainland and Europe (Buch 1819). In this context, and in his later book-length account (Buch 1825), he also reflected on a central biological subject, the manner in which the stem species of a genus becomes divided into separate species. It is this discussion that makes him a true "Darwinian before Darwin," as he was called by Günther (1900). Jürgen Haffer (pers. comm.) reviews the history of the biological species concept and discusses in some detail Buch's research and his significance as the founder of the biospecies concept and as the first exponent of the theory of geographic (allopatric) speciation.

Buch (1825: 132-133) wrote: "The individuals of a genus spread out over the continents, move to far-distant places, form varieties (on account of differences of the localities, of the food, and the soil), which owing to their segregation cannot interbreed with other varieties and thus be returned to the original main type. Finally these varieties become constant and turn into separate species. Later they may reach again the range of other varieties which have changed in a like manner, and the two will now no longer cross and thus they behave as two very different species" (cited from the translation in Mayr 1942: 156; see also Mayr 1963: 483 and Kottler 1978: 285). This is the earliest brief yet clear discussion of what was later known as the biological species concept of the modern synthesis of evolutionary biology.

Buch's definition is the most original theory of species and speciation of the early 19<sup>th</sup> century, even by choosing a few different terms we can hardly improve on his central tenet and have the BSC as it was defined more than a century later. In analysing the essential features of Buch's definition we find that, first, it is a non-essentialistic concept. Buch considered species not to be types but populations or groups



of populations consisting of biologically unique individuals. Thus, unusual for his time, which was dominated by typological thinking, he shifted to population thinking long before Darwin laid the foundation with his new concept of natural selection. Buch defined species not in terms of degree of morphological differences but rather stressed that they are separated by a (bridgeless) reproductive gap. And, second, he suggested a model of geographical speciation, starting from the notion of geographical variation without fixed species limits and the idea that geographical isolation is needed to permit species differences to “become constant.”

### LEOPOLD VON BUCH'S LEGACY

Leopold von Buch's (1819) first publication of his critical definition of species and his theory of speciation later fell into oblivion. However, in 1825 he published a large book on the natural history of the Canary Islands (Buch 1825) which, in a French translation (1836), was read, for example, by Charles Darwin [1809-1882] and Alfred Russel Wallace [1823-1913]. Darwin mentioned the “admirable discussion” of Buch in his Notebook B of 1838 (Kottler 1978), while Wallace, having read and appreciated Buch's book, translated the same critical paragraph into his “Species Notebook” in 1857 (Beddall 1968, Kottler 1978). Without a doubt, he fully appreciated the observation on geographical isolation given his own experiences in the Indo-Malayan Archipelago. However, like Darwin, Wallace focused mainly on how selection drives evolution over time, and not so much on the mechanism of (geographical) speciation.

Albert Mousson [1805-1890] of Zurich, Switzerland, a well-known malacologist who had a personal connection to Leopold von Buch as a student (for a brief biography see Meier 1993), devoted an entire introductory chapter in his book on the “Land and Freshwater snails of Java” to the concept of species in conchology. There he defined species as “all normally formed individuals which interbreed fully fertile with one another” and as “the total of individuals, interconnected by descent and reproduction, maintaining unlimited reproductive capabilities” (Mousson 1849: 3). Way ahead of his time, he also stated that “nature provides us as independent organisms only with individuals, which are comprised by the collective name of the species. Nevertheless, this concept is not a mere abstraction, but has a certain reality in nature” (1849: 2, my translation). Mousson emphasized species as objective entities, not just as artificial units. He distinguished species clearly from subjective categories such as genera, family, and order, and he used, following Buch, reproductive isolation as the decisive criterion for the assignment of species status. In his opinion, naturalists should not create species, but detect them. By recogniz-

ing the geographical variation potentially leading to speciation, Mousson also gave up the typological view of fixed species limits. Interestingly, although Mousson's collection comprised about 200,000 shells of about 8500 species and subspecies, of which he described 450 as new, he never designated a single specimen as “type” and, therefore, his collection only consists of type series (Meier 1994). Thus, although a malacologist was among the first to suggest the application of reproductive isolation for a species definition, Mousson's insight was lost for over a century in malacology. As pointed out by Giusti and Manganelli (1992), who cited some examples from those who work with terrestrial and limnic molluscs, in everyday practice the typological approach (i.e. regarding as species only what can be morphologically defined) is still widely used as if Mousson was never read or understood.

A couple of 19<sup>th</sup> century naturalists, among them Henry Walter Bates in England, Moritz Wagner and Ernst Haeckel in Germany, and Benjamin Walsh and John Thomas Gulick in America, also viewed species as interbreeding populations, but they never developed this theme in further detail (Haffer 1992). For example, the naturalist-missionary Gulick [1832-1923], who studied the Hawaiian tree snails of the family Achatinellidae, became not only a critic of deterministic adaptationism, but also an early advocate of the importance of isolation in the generation of new species (Reif 1985). He later stated that “the soundness of the claim that the prevention of free crossing is a necessary principle in the divergent evolution of races and species” gained wide recognition among biologists of the early 20<sup>th</sup> century (Gulick 1905: 51). However, it was the publications of Rensch (1929, 1934) and Mayr (1940, 1942) that established speciation and the criteria involved in a biological species concept in the most comprehensive way (see Mayr 1963, 1982, Haffer 1992).

### WHY DO SPECIES MATTER?

In the context of the question of what species are, it is certainly not helpful that the word “species,” deriving from Latin “specere,” means “to see” or “to recognize.” However, species are more than what a biologist recognizes. Because the discussion of no other concept in biology is hampered more by misunderstanding and confusion of terms, a careful application of terminology (i.e. use of language) is a prerequisite in this debate, as was pointed out explicitly by Ax (1984), Ghiselin (1984), Mayr (1988a, 1997) and Wägele (2000). Constructive discussions can only be carried out based on clearly defined concepts. The debate about species, in my opinion, has not seldom been approached with the dangerous attitude of at best neglecting, at worst ignoring,

the admittedly vast amount of literature and its theoretical, biological, and philosophical implications.

Unfortunately, it is impossible to review here some of the indispensable theoretical aspects of the species question, for example whether species are artificial and arbitrary constructions or have an actual existence in nature (see Burma 1949, Ghiselin 1966, 1975, 1997, Löther 1972, Griffiths 1974, Hull 1976, Willmann 1985, 1991, Mayr 1988a: 335-358, Nelson 1989, Mallet 1995, Bock 2000). The present paper assumes *a priori* that species are real, that is, natural and evolutionary entities. Accordingly, species exist whether we can recognize them or not, and they are not mere imaginary or hypothetical constructs or mere concepts to serve our subjective understanding of nature. I strongly feel that we should indeed stick to perceiving species as naturally distinct units, that is, as objective realities, not just as abstractions.

Another fundamental discussion rests with the question of whether species represent "classes" or "individuals" (see Hennig 1950, 1966, Mayr 1963, 1982, 1988a, 2001, Löther 1972, 1991, Griffiths 1974, Ghiselin 1966, 1975, 1988, 1997, Hull 1976, Mishler and Donoghue 1982, Willmann 1985, Caplan and Bock 1988, de Queiroz and Donoghue 1988, de Queiroz 1995, Baum 1998, Mahner 1998, Bock 2000, Gould 2002). The typological and nominalistic approach considering species as classes ("natural kinds"), as constant types that are separated from any other species by an unbridgeable gap, is to be regarded singularly unsuited to evolutionary and population biology, "where one finds not classes but aggregates of unique individuals, that is, populations" (Mayr 1997: xii) (for an account on the history of the development see also Mayr 1982). Although this particular aspect of species should be of relevance for systematists, for the sake of brevity here the reader is referred to an in-depth discussion of the species-as-individuals theory to reviews and literature therein provided by Rosenberg (1985), Mayr (1988a), and Ghiselin (1997), with a clarification of the metaphysical foundation attempted most recently by Bock (2000).

Clearly the most fundamental, albeit often neglected distinction in this context is between (1) the definition and concept of a species (or German *Artbegriff*) and (2) the species taxon (that is, natural object, or particular) ranked as a category in the Linnaean hierarchy, referring to the central but often overlooked aspect of "conceptualization" versus "categorization." This distinction between the two meanings of the word "species" has explicitly been pointed out by Hull (1965, 2002) and subsequently discussed in Mayr (1982, 1988a, 1996, 2001), Willmann (1985), Frost and Hillis (1990), Bock (1995), and most recently Hey (2001a, 2001b), but see Mishler and Donoghue (1982) and McKittrick and Zink (1988).

Although often confused, species concepts (the meaning of species in nature) and species taxa (as zoological objects to

be categorized in an ordering system) are completely different things. Indeed, it is important to distinguish species as a theoretical notion (i.e. concept) from the species category within taxonomy to which species taxa are assigned. Although the idea is that species taxa are unique and fundamental and that the species is also a category within the Linnean hierarchy, we have to be aware that, in contrast, above the species level all other higher categories are not objectively defined, but practical constructs for the purpose of ordering and classifying groups in nature. This categorization as a purely taxonomic procedure is often confused with the conceptualization, that is, the theoretical idea of what species actually are. Being particulars, only species taxa can be described and delimited against other species taxa.

Thus, as Mayr (1996) pointed out, there are actually two different sets of species problems, one being the problem of how to define the species (which species concept to adopt) and the other being how to apply this concept in the demarcation of species taxa. Accordingly, although we describe and recognize species taxonomically, this is only the best approximation of a "real species" we can get. We can only hope and strive to accomplish that our category "species" match up with the real evolutionary groups that are localized in space and time. As naturalists we discover species. We do not create them, however, because they are already there.

In this context, the inconsistent and often confusing way in which the term and concept of species are used in many malacological studies is disturbing. Most taxonomic revisions, for example, do not explicitly or implicitly state the author's concept of species, leaving it to the reader to speculate on the theoretical background from which the author is approaching the case. Other studies at least mention the common problem of species delineation, but define terms such as "species," "genetic species," and even "super-species" in unconventional ways, inconsistent with any other definition generally used. One example to illustrate this is Ponder *et al.* (1994: 569) in which species are "defined" as "the outgroup and the two ingroup taxa restricted to their type locality," while genetic species are defined as "non-interbreeding genetically definable taxa not readily recognized using morphological data." Although particularly in malacology representatives from individual populations can often be discriminated using shell or other morphological characters, the existence of distinct biospecies remains unclear, as does the conceptual basis used by the researchers.

The choice of which species concept to apply is fundamental to systematics and malacozoology, since phylogenetic, ecological, and other studies are only as good as their underlying data and assumptions. The species concept and the agreement whether species are "real" also have a serious impact on the way we organize collections, view the world,



and talk about biodiversity and conservation. For example, any discussions of species richness, any inventory of the fauna, will be seriously dependent on the outcome of this debate. Only if we accept species as real will speciation be a real process and a meaningful problem. Consequently, we need to study the role of reproductive isolation in speciation and look for the geographical context in which species exist.

### FROM STAMP-COLLECTING TO EVOLUTIONARY BIOLOGY

Because a species is apparently much easier to recognize than to define, the crucial questions remain: What constitutes species and how do we delimit them? Paradoxically, in systematic practice the most widely used methods are still essentially morphological, i.e. species are treated as phenotypic (and/or genotypic!) units instead of real genetically cohesive communities. As long as naturalists assumed that species were constant with fixed limits and were consistently regarded as separate and independent creations (as was done in and long after Linnean times), this substantially typological approach did not cause theoretical problems.

However, the crucial question of variation increasingly gained attention among naturalists during the second half of the 19th century. With the general acceptance of the Darwin-Wallace theory of evolution, in particular in its modified version of the modern synthesis (reviewed in Mayr 1982, 1991), geographical variation became a central element for the understanding of evolution and speciation, eventually resulting in the increased recognition of the biological species concept (BSC). Under the BSC species were no longer considered as artificial sets defined by phenetic attributes, but as real genetic units, in theory, two taxa form separate species if they are reproductively isolated from one another and incapable of exchanging genes. With the tenet of species being populations of interbreeding organisms, many zoologists started to think about species as being localized in space and time, resulting in numerous studies that paid much attention to phenotypical (and most recently also genotypical) variation in the geographical context.

Research and observation *in situ*, the “geographical principle” that was established explicitly by Alfred Russel Wallace (thus dubbed “Wallace’s program” in Glaubrecht 2002) provided the geographical key for the study of the spatial pattern of the distribution of animals as well as for understanding the origin of species and the mechanisms of speciation. It is these geographical data that facilitated insights into complex phenomena in evolutionary biology such as natural selection, faunal regions and their delineation, endemisms and radiations, *formenkreise* and superspecies, as well as the principle of peripheral isolates and the

concept of allopatric speciation. Accordingly, providing the knowledge on geographical occurrences of faunal and floral elements over vast areas of the globe in concert with their geographically related variation has to be considered the main contribution of travelling naturalists from Darwin and Wallace to Stresemann, Rensch, and Mayr, who later became instrumental in the development of the modern synthetic theory of evolution (Glaubrecht 2002).

It was the naturalist-explorers’ demonstration that not only do individuals exist in nature but directly intergrade and vary geographically within populations. The discovery and documentation of the existence of discontinuities in the natural interpopulational variation of morphological and other markers eventually led to the awareness of the importance of the long-neglected geographical factor, not only for variation and species delimitation, but for speciation and evolution in general. As mentioned above, an early exception to this common neglect during the 19<sup>th</sup> century was Moritz Wagner (1868, 1889), who pointed out the importance of geography for speciation. Later, Bernhard Rensch (1929) and Ernst Mayr realized how crucial the presentation of a massive documentation in favor of geographical speciation would be, given the then prevailing ignorance of the role of geography in zoology (Glaubrecht 2002).

Recently, molecular genetics has brought some astounding improvements and many new insights into the biological nature of species, but still no resolutions to the species problem. Nevertheless, it is the spatial aspect and the relations along contact zones in concert with microgeographical differentiation that are most promising for contributing new facts towards a solution of the species question.

### THE BIOLOGICAL SPECIES CONCEPT

#### Definition and historical development

The concept of biological species is based on the observation of 19th century naturalist-explorers that populations vary geographically to different degrees and that populations of different species at a given locality coexist but do not interbreed with each other. The most valuable working definition of a biological species is that of Ernst Mayr: “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr 1942: 120).

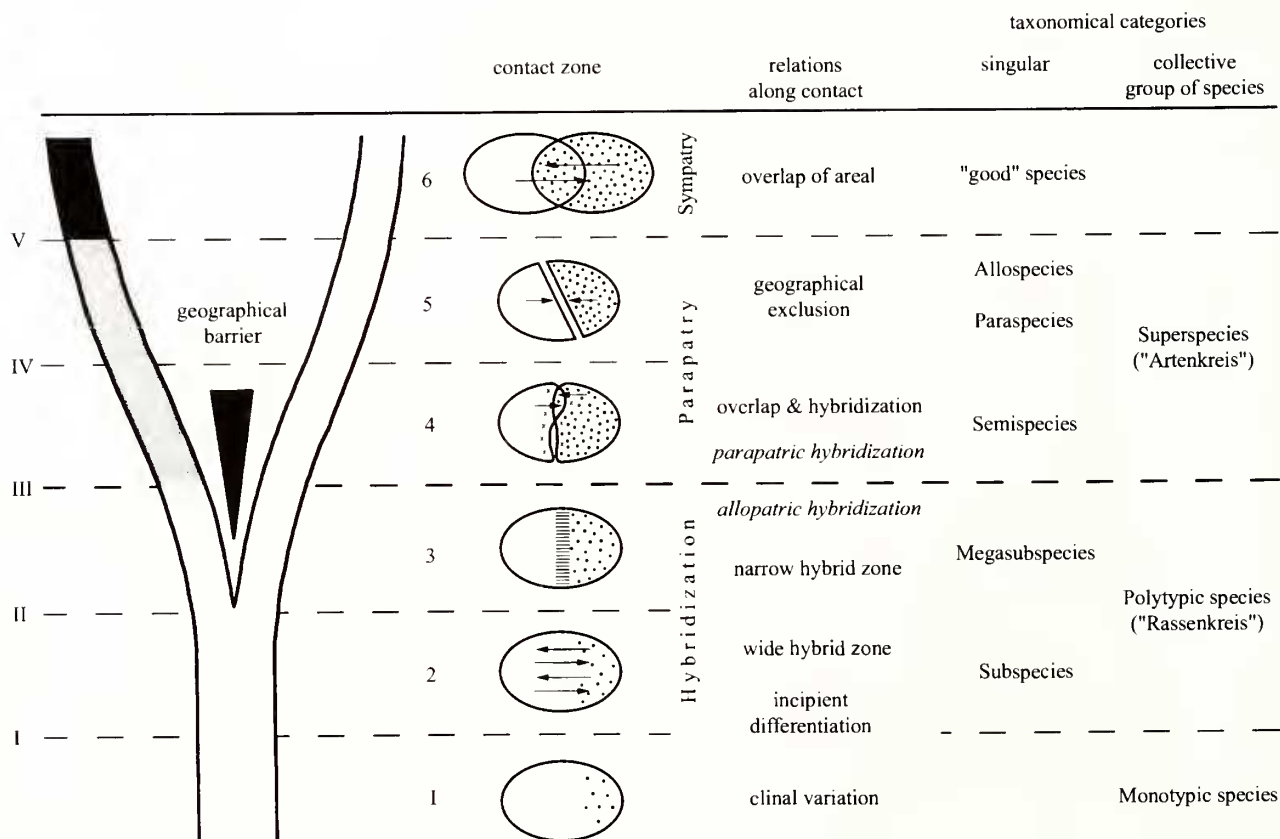
Mayr was significantly influenced by a group of ornithologists at the Berlin Natural History Museum, especially the curators Erwin Stresemann [1889-1972] and Bernhard Rensch [1900-1990]. This “Berlin circle” followed a research tradition of ornithologists started by Henry Seebohm [1832-1895] and Ernst Hartert [1859-1933] in England (Haffer 1991, 1992, 1995a, 1997a, 1997b, 1999, 2001, Haffer *et al.*

2000). After gaining many insights from his field experience in New Guinea and the Solomon Islands in 1928-1930, Mayr followed the Berlin tradition of delineating species in a geographical context in his works of the 1930s and 1940s.

In addition, Mayr (1942, 1963) proposed that new sister taxa arise when an ancestral species is subdivided into geographically separate populations that subsequently evolve independently. According to the much favored allopatric model of speciation, the separated forms may accumulate many genetic differences and isolating mechanisms are acquired by incipient species over time so they no longer interbreed when they subsequently meet again (Fig. 1). Thus, new species are not the result of ad hoc selection but of a change of function of properties acquired during the preceding isolation.

As a consequence of Mayr's (1942, 1963) synthetic works, the criterion of reproductive isolation, including the

importance of geographical variation, separation (i.e. geographical isolation), and the non-applicability of the degree of (phenotypic) distinctness, was widely accepted as most valuable for defining biological species. The BSC was long considered as best corresponding to the organic discontinuities observed among organisms living in one area. Linking zoological systematics with population genetics, Mayr's BSC became not only a key element of the modern synthesis of evolutionary theory, but was later adopted as the official species definition in conservation legislation, such as the US Endangered Species Act. Using this biological definition of species as interbreeding groups provides an objective and non-arbitrary procedure for determining species status. Reproductive isolation not only represents the only objective criterion available to date, but the evolutionary most meaningful one, and should, thus, be considered the ultimate decisive element in case of conflicting evidence (Mayr, 2000).



**Figure 1.** Classifying borderline cases of the microtaxonomic differentiation between subspecies and "good" species. The terminological framework of components in the speciation process is given (under the BSC) as discussed in the text. Stages 1-6 are intermediates in the continuous differentiation of groups of populations. Roman numerals mark the different levels of species limits according to the relevant species concepts, with I-II indicating "cladistic" species categories: I—phylogenetic species, II—evolutionary species, III—biological ("multi-dimensional") species, IV—species under the recognition concept, V—zoogeographical species [Adopted and combined from Haffer (1985: 53, fig. 1) and Haffer (1992: 116, tab. 1)].



### Criticism

Even in view of the fact that interbreeding in nature is the finest possible evidence for evolutionary units, the BSC was often held to be non-universal, non-operational and non-applicable (for example Cracraft 1983, Endler 1989, Hull 1997, Mayden 1997, see also more recent discussions in Eck 1998, Wheeler and Meier 2000, Hey, 2001a, 2001b). The BSC was also accused of confusing pattern and process with a bias towards a particular type of speciation. Accordingly, Mallet (1997) criticized that “by postulating an ideal species, rather than a practical approach to sorting actual taxa, Mayr opened a Pandora’s box.” It was even claimed that the BSC altogether “is not very useful” (Schilthuizen 2001: 19). However, difficulties in the application of the BSC (for example those arising from allopatry, lack of information or cases of incomplete reproductive isolation and hybridization) in themselves do not detract from the validity of the concept. Another cause for misunderstanding the value of the BSC is the lack of distinction between species concept and species taxon (or species category), as discussed above.

Admittedly, there are limitations and a genuine inapplicability of the BSC in the cases of asexuality (uniparental reproduction) and allopatry. Indeed, the BSC is only applicable to organisms reproducing bisexually. For those organisms, however, that reproduce non-bisexually, either completely unisexually (parthenogenesis) or asexually, the agamospecies becomes available, rendering the claim of only a single universal species concept inappropriate. For a discussion of the species concept in parthenogenetic taxa see Maslin (1968), Sudhaus (1984), and Häuser (1987). The existence of reproductive isolation in nature can only be determined with certainty when taxa are sympatric. Given the gradual process of speciation, non-continuous populations may or may not have reached the level of biological species. The status of such taxa, including subspecies belonging to the same species or paraspecies, allospecies, and semispecies (Fig. 1), can be determined by inference only (Mayr 1997, 2001). These inferences have to be made within a taxon-specific framework using the degree of morphological and other differences or, with recent advances in molecular methods, by comparison of genetic distance. Making those inferences is advocated here as necessary and logical procedure that follows from the theory of the BSC. Although McKittrick and Zink (1988: 3) rightly called the inapplicability of the BSC to allopatric forms “an underemphasized problem because there are thousands of allopatric populations,” the inability to treat allopatric populations objectively and provide a foolproof system for the correct assignment of isolated populations or other cases of evolutionary intermediacy is inherent in all other species concepts as well.

The BSC is most often criticized as being non-

dimensional. However, by viewing a species as existing and extending its populations in a geographical framework, the BSC actually is two-dimensional. With this horizontal notion a biological species appears as a real unit in nature. Although the BSC is admittedly not vertical, that is not primarily a historical concept, if we add the time dimension, three-dimensionality is gained, as suggested by the chronospecies concept. This latter concept (artificial delimiting of portions of phylogenetic species lineages), however, is essentially nothing more than a morphospecies concept applied to fossils. Accordingly, the chronospecies concept uses the criteria of the BSC combined with the morphological approach in geological time (Reif 1984, Willmann 1985, see also papers in Eck 1998).

### Expanding the concept

Emphasizing again the distinction between species concepts and species taxa (as discussed above), we find that the species concept is based on the non-dimensional situation, while the species taxon is multi-dimensional. Adding the dimensions of geography and time permits a way to treat populations taxonomically. Applying the ideas of the BSC and, in addition, subsequently testing how many populations and presumed subspecies (due to their distinctness) actually deserve species status even in allopatry, this procedure became a valuable and more heuristic endeavor, in ornithology, for example, than the often meaningless dispute over naming “species” or “subspecies” in allopatric and/or parapatric situations. The last decades have seen the development of the methodological tools to treat the various instances of evolutionary intermediacy. To accommodate taxonomically these stages of the microgeographical differentiation process in concert with the BSC, a terminological framework has been developed, in particular in ornithology (Fig. 1). Terms such as para-, allo-, semi-, and superspecies proved most valuable in the context of zoogeographic and phylogenetic studies, and entire faunas have been studied utilizing this approach (see Haffer 1985, 1992, Amadon and Short 1992, Sibley and Monroe 1990, see also literature cited therein for examples from ornithology). Adequate systematic inferences and the application of allo-, semi-, and syn-species of a superspecies is advocated, for example, by Mayr (1942, 1963), Amadon (1966), Sudhaus (1984), Haffer (1986), Sibley and Monroe (1990), Mayr and Ashlock (1991), Glaubrecht (1993, 1996, 2000), and Helbig (2000).

### THE DEBATE CONTINUES

#### How to delimit species in a cladist’s world?

The last two decades have seen a particularly active phase of debate about how to define and delineate species in

a cladist's world. Phylogenetic systematics, as proposed originally by Hennig (1950, English translation 1966, see also Ax 1984 and Wägele 2000), and particularly its application and recent computation utilizing advanced methods in bioinformatics and technology by cladists, produced a revolution in systematics. Unquestionably, the rigorous application of cladistic analysis had a major impact also on many other aspects of systematic biology, resulting in "tree thinking" (O'Hara 1994). Because the BSC was considered insufficient for this purpose, phylogenetic thinking, or the cladistic approach to nature, necessitated the re-evaluation of concepts in systematics, with cladistics recognizing the importance of a species concept that serves their methodology of branching patterns and clades defined by synapomorphies, leading to "(re) inventional word games," as Avise (2000b: 1831) rightly noted in his elegant and eloquent book review on "the speciational wonderland." Currently, there are 22 ways to view and perceive what a species is, according to a review by Mayden (1997); Hey (2001b) lists 24 concepts. While the battle over the best cladistic species concept continues among cladists, proponents of the BSC, especially Mayr (2001), denied that any of the new phylogenetic concepts is legitimate, since "none of the authors of these new concepts has understood the difference between a species concept and a species taxon. Instead of new concepts, they have proposed new operational criteria of how to delimit species taxa."

Following a suggestion by Haffer (1992, 1998) and Gittenberger (1972), who both tried a systematization among the multitude of species definitions instead of a mere compilation, I will distinguish here between "horizontal" and "historical" species concepts. Although a species as defined by the BSC can be viewed as a horizontal cross-section of a phyletic lineage at any given time, a historical species concept results in the vertical delimitation of species as suggested, for example, under the Hennigian Species Concept (HSC) (Meier and Willmann 2000), the Evolutionary Species Concept (ESC), and (implicitly) under the Phylogenetic Species Concept (PSC). Proponents of the HSC, ESC, and PSC consider species to be parts of a "vertical" evolutionary lineage between two consecutive cladogenetic events (that is speciation and/or termination through extinction). The following brief review will restrict itself to the vertical concepts ESC and PSC, other concepts are considered of minor importance, because they reflect only special aspects with slightly changed emphases.

### The Evolutionary Species Concept

Simpson (1961: 153) suggested defining species as "a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Later, Wiley (1978: 18) proposed in a slightly revised version that "a species is a

single lineage of ancestral descendent populations of organisms which maintains its identities from other such lineages and which has its own evolutionary tendencies and historical fate." More recently, Wiley and Mayden (2000) have re-defined and defended the evolutionary species as "an entity composed of organisms which maintains its identity from other such entities through time and over space and which has its own independent evolutionary fate and historical tendencies."

Although considered relevant for both living and extinct groups and to sexual and asexual organism, the ESC is non-operational and subjective (that is, containing undefinable criteria rendering them useless in practice), and even Simpson himself has abandoned his own concept as being rather nebulous for systematic purposes (Reif 1984, O'Hara 1993, Mayr 1992, 2001). How, for example, is one to describe and determine "evolutionary tendencies" or "historical fate" of a population or taxon? Nevertheless, the ESC is still supported and frequently recommended (e.g. Maslin 1968, Wiley 1980, 1981, Ax 1984, Willmann 1985, Otte and Endler 1989, Frost and Hillis 1990, Mayden 1997, Peters 1998). However, the ESC failed to provide its main objective, namely a clear delimitation of a species in the time dimension that turned out to be illusory in all cases of gradual species transformation, as is illustrated in particular by the classical *formenreihen* of freshwater gastropods (see Willmann 1981, Williamson 1981, further discussions in Reif 1984, Eck 1998). In essence, the ESC is a typological morphospecies concept that is not operational; it can only assume that characteristic features are consistent and thus diagnosable throughout the entire historical existence of the evolutionary lineage.

### The Phylogenetic Species Concept

Cladistic methodology views the world as branching patterns. According to this philosophy, every lineage starts and ends with a branching event (speciation) or its extinction and is characterized by at least one autapomorphy. This view led to the need for a species concept consistent with phylogenetic principles. The reproductive criterion (i.e. breeding compatibility) is considered inappropriate among cladists to group organisms into species. Instead, the existence of unique patterns of shared and diagnosable characters is proposed and defended as a sufficient criterion.

Espousing PSC as alternative to the BSC, for example, Cracraft (1983: 170) defined species "as the smallest diagnosable cluster of individual organisms within which there is a parent pattern of ancestry and descent." He later defined species under the PSC as "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent" (Cracraft 1989: 34-35). For a historical review and application of the many versions of the PSC see Mishler and



Brandon (1987), McKittrick and Zink (1988), Mayden (1997) and Mishler and Theriot (2000).

One of the most serious problems with the PSC is that there are too many versions, which leads to confusion about the specific definition. Regrettably, irrespective of the two decades of debate, cladists have failed to set or agree on any standards for what to consider a "phylogenetic species." This lack of consensus is both a problem for communication and acceptance, and is a source of much confusion and many misconceptions, which hampers scientific progress. Mayden (1997) sorted out two main approaches, the diagnosable version and the monophyly version of the PSC, the latter stemming from the debate of cladists whether the concept of monophyly should be extended from higher categories to the species level (de Quieroz and Donoghue 1988, Nixon and Wheeler 1990).

### **The diagnosable version**

In the definition of Nixon and Wheeler (1990: 218) a species is "the smallest aggregation of populations (sexual) or lineages (asexual), diagnosable by a unique combination of character states in comparable individuals (semaphoronts)." Because this definition is character-based it renders a phylogenetic species analogous to a morphospecies, even if now allowing to do so on an additional level, such as the molecular features. Accordingly, using the increasingly improved methods of molecular genetics, it currently becomes more and more standard procedure to characterize each and all geographically separated populations by apomorphic features (i.e. sequence differences), with smaller populations more easy to track than large polymorphic ones. In conclusion, those populations which turn out to be consistently diagnosable by characters or character combinations recognizable by ordinary (= arbitrary) morphological means and/or molecular means (single fixed nucleotide base pairs) are considered as species under the PSC.

### **The monophyly version**

Rosen (1978) stated that "a geographically constrained group of individuals with some unique apomorphous characters, is the unit of evolutionary significance." More recently, Mishler and Theriot (2000) defined species as "the least inclusive taxon recognized in a formal phylogenetic classification." Accordingly, "taxa are ranked as species, because they are the smallest monophyletic groups deemed worthy of formal recognition." This concept equates species with monophyletic units and speciation with character transformation. There are a few problems with monophyly in this context, for example, the question of whether species are, must, or can be monophyletic (Wiley 1981, Willmann 1983, McKittrick and Zink 1988, Wheeler and Nixon 1990).

Establishing "monophyly" for species has proven difficult in practice, as Nelson (1989) admitted.

Generally, PSCs have been criticized for three different reasons. In addition to being (1) typological and to diagnose evolutionary units on the basis of (partly trivial) characters, they are (2) arbitrary and reductionistic in the sense that they not include important biological criteria, and are (3) leading to the recognition of too many species. Apart from the question of what actually is "phylogenetic" about a species, for example, Mayr (2001: 167) criticized the various phylogenetic species concepts as "simply typological prescriptions of how to delimit species taxa." Starting from the conviction that without clear-cut definitions no progress in the clarification of concepts and theories is possible, it is not helpful that in the last two decades so many cladists have come up with several more or less divergent definitions of the phylogenetic species concept. Often even the same authors have different formulations and wordings at different times, without reaching any compelling synthetic consensus. This results in confusion of what an author means when referring to a species under the PSC and it certainly defeats the cladists' claim to provide with the PSC a viable alternative to the BSC. Given the purported demise of the BSC, the recent debate, illustrated in Wheeler and Meier (2000), reveals that the "revolutionaries," as Avice (2000b) stated, have not come up with something much better.

In addition to the often rather nebulous and vague usage of words in the PSC definitions, any focus on diagnosable differences between phylogenetic lineages, not necessarily representing populations, renders it reductionistic and non-biological, because it ignores the relationship to other populations or taxa within a geographical and historical context. The operational orientation of the PSC (serving better diagnosability) not only leads to subjectivity, it also renders the PSC a clearly typological concept close to essentialism, which had been overcome with the modern synthetic theory of evolution. As a result, the PSCs will eventually lead to the same ballooning of species numbers as observed in the 19<sup>th</sup> century.

In combination with the arbitrariness of changing delimitation of species under the different versions currently available, the PSCs render comparative studies of faunas and speciation processes hazardous. Only very disputably is the PSC truly a species concept, i.e. in the sense of having any relevance to a species as a natural entity in nature. Defined in this way, a phylogenetic species does not play any role in the ecosystem nor seem to have any interaction with other populations of the same species or with other species, but only serves as a description of a taxon on a cladogram. In addition, the various stages of differentiation in geographically vicariant populations or taxa are not distinguished taxonomically.

Because of the subjectivity of delineating populations in the patchy, allopatric situations of continental areas, the application of the PSC under the diagnosability version endangers consensus among systematists and, therefore, taxonomic stability (see critique in Eck 1998, also Snow 1997, Haffer 1995b, 1998, Wheeler and Meier 2000). Irrespective of these problems, the PSC has been widely stated as providing an objective species concept. It was strongly advocated, first by ornithologists (for example see Cracraft 1983, 1989, McKittrick and Zink 1988), but later also by other practical zoologists (see Kottelat 1997 and Lydeard *et al.* 2000 for two examples).

### Implications and consequences

Proponents have failed to develop a single useful, standard definition for a "phylogenetic species" that secures congruent use. In addition, the PSC is an attempt to combine two widely disparate concepts, namely monophyly and diagnosability, into one species definition, which increases the number of practical and theoretical problems (see for example Sluys 1991). Thus, with respect to the alternative definitions under the PSC, the criteria given do not achieve the demanded degree of objectivity. Ultimately, the immanent subjectivity of the definition will result in arbitrary species delimitations.

In contrast, the criterion of reproductive isolation under the BSC provides an objective means of separating sympatric species. This criterion also represents the causal factor that produces and maintains discrete entities. Avoiding an inflation of "species" by naming even slightly differentiated forms or populations with unbalanced degrees of differentiation, which can happen using the PSCs, the BSC makes an attempt to delineate taxa as species with respect to the same degree of differentiation.

When systematists apply a narrow morphological species concept, they arrive at higher numbers of species. For an example from birds see Figure 2, for other examples from fishes and insects that apply the PSC see Kottelat (1997) and Packer and Taylor (1997), respectively. Thus, so-called "wide" versus "narrow" approaches of delineating species have direct consequences for the assessment of biodiversity and conservation. As a consequence of the perception of species as diagnosable units, the application of PSCs will result in a great proliferation of species and inflate the biological diversity on the lowest taxonomical level, even if one accepts only phenotypic differences and not molecular genetic differences.

In conclusion, the PSC is certainly not an improvement. Although not perfect, the BSC is still the most useful and meaningful concept, while PSC lacks objectivity and is a step backward to the days of typological thought. Not by accident, the BSC became the "working definition" of species

among most population and evolutionary biologists for most of the last century, although it was formulated not for convenience but for its correspondence to natural phenomena, as Coyne *et al.* (1988) pointed out. Taken together, the problems with the BSC are fewer than those faced by other species concepts, particularly those based on morphology. Therefore, the difficulties of applying the BSC are not such as to justify its rejection in favor of other, logically and biologically worse concepts. The BSC is to be favored because it is the only definition that is based primarily on the biological significance of a species.

### TWO EXAMPLES FROM FRESHWATER GASTROPODS

Initially in malacology (when it was perceived essentially as conchology), a plethora of nominal species were described, followed by only a slight tendency to reduce the numbers of species after population thinking was implemented in some areas of the study of molluscs. Generally, it was concluded that much of the observed conchological variation actually represented population-level phenomena. However, in the absence of studies explicitly focussing on reproductive isolation in sympatry, most taxonomic decisions are still largely subjective and primarily based on morphology.

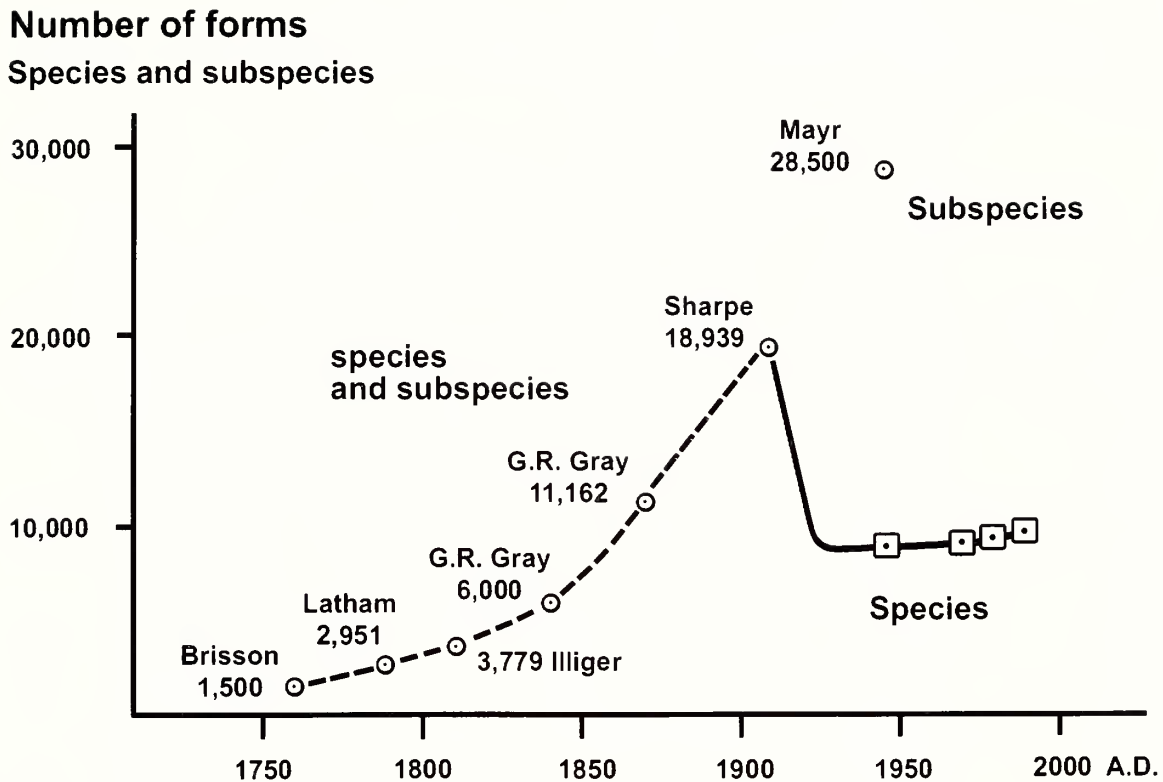
Because more freshwater biotopes occur in isolated areas than do marine or terrestrial ones, populations of freshwater gastropods tend to be isolated (Rensch 1929, Hubendick 1954, Meier-Brook 1993, Glaubrecht 1996). This discontinuous distribution not only leads to morphological variations in isolated populations and microgeographic races, but consequently also results in the naming of nearly each of these populations as distinct species under typological-morphological species concepts. This will also be the case under the PSC, because these concepts do not take into account biological phenomena such as geographical distribution and genetic cohesiveness, even of temporarily separated populations.

Two case studies of freshwater gastropods of the former "melaniid species basket" ("Melaniidae" = Thiaridae *sensu lato* of the superfamily Cerithioidea, see Glaubrecht 1996, 1999) illustrate this point, using taxa of *Lavigeria* Bourguignat, 1888 from Lake Tanganyika (which should be grouped as belonging to the Paludomidae instead of Thiaridae *s. str.*, see Glaubrecht 1999, Strong and Glaubrecht 2002), and the North American Pleuroceridae.

#### Case 1: "Le Bourguignatisme"—an example from Lake Tanganyika

One of the most unhappy episodes in the history of malacology is the French school of the so-called "Nouvelle





**Figure 2.** Implication of applying different species concepts. Marked by the works of ornithologists during the last 250 years the increase of numbers of species and subspecies of birds is shown, culminating in the recognition of 18,939 species around the turn to the 20<sup>th</sup> century. Applying the multidimensional species concept (under the theory of the BSC and influenced by the “Berlin circle” and Ernst Mayr, see text), eventually halted this process after 1900. Reversing the situation during the 1920s and 1930, many morphospecies were reinterpreted as subspecies and combined in more widely conceived biological species taxa. Immediately, this resulted in a precipitous decline in the number of species recognized. It was the emphasis of the existence of closely related allopatric and parapatric species (together forming a superspecies) that led to a moderate stability regarding species numbers during the 1930s and 1940s, and to an estimated total number of known birds of today around 9700 species. This process, starting during the late 1920s, when geographically representative biospecies were discovered, can be aptly called a “quiet revolution” in systematics, that is still missing in malacology [after Haffer 1992: 147, fig. 4].

École,” with Jules-René Bourguignat [1829-1892] as its main proponent. Bourguignat considered as distinct species (and merited a name to) taxa that could be distinguished on the grounds of three or more constant characters. Called the “bête noir of European malacology” (Dance 1970) and the “great species manufacturer” (Kobelt 1881), Bourguignat was the most radical among conchological splitters. Unable to comprehend or accept the concept of species as a biological entity, he regarded species as abstractions that did not exist outside his imagination.

One of Bourguignat’s special interests was the so-called thalassoid (marine-like) molluscan fauna of Lake Tanganyika. Someone who could conjure up dozens of novelties from an average European lake or make 20 species out of a well-known species of European freshwater mussel, could work miracles with these thalassoid gastropods. Based on

collections from various French naturalists, Bourguignat described 75 new “species” and proposed 9 new genera in his final masterpiece, the “Histoire malacologique du Lac Tanganyika” (Bourguignat, 1890). For example, he split *Lavigeria* as we know it today into five genera and compiled 51 named species for it, introducing 46 new species between 1885 and 1890 (another 7 species were described in subsequent decades). In contrast, only one or two species, *Lavigeria nassa* (Woodward, 1859) and *Lavigeria grandis* (Smith, 1881), respectively, were accepted by Leloup (1953) and Brown (1980, 1994) under the (implicit) application of the BSC. For an illustration of the taxonomic history of *Lavigeria* see Table 1.

Bourguignat and his colleagues can be excused by the fact that they lived when there was little agreement over the species problem. However, this situation is quite different from today with some systematists only being dissatisfied

**Table 1.** The taxonomic history of *Lavigeria*, a thalassoid gastropod endemic to Lake Tanganyika, East Africa, illustrates the changing number of species (and generic) names applied under different taxonomic concepts.

| Author                      | No. of species | No. of genera |
|-----------------------------|----------------|---------------|
| Bourguignat (1890)          | 51 species     | 5 genera      |
| Pilsbry and Bequaert (1927) | 22 species     | 1 genus       |
| Martens (1897)              | 10 species     | 1 genus       |
| Leloup (1953)               | 2 species      | 1 genus       |
| Brown (1980, 1994)          | 2 species      | 1 genus       |
| Michel (2000)               | 20+ species    | 1 genus       |
| Todd and Michel (2001)      | 30+ species    | 2 genera      |

with the answers already available to the species question. It is interesting to note that this dissatisfaction has again resulted in an increase of the number of named species in *Lavigeria*. While only two species were accepted since Leloup's (1953) treatment, more recently the existing morphological disparity in Lake Tanganyika has been approached by naming the smallest diagnosable units (as suggested, for example, under the PSC) and implying a local radiation within this genus (e.g. Michel 2000, Todd and Michel 2001). Regrettably, not only is Bourguignat's typological approach repeated this way, but also a general weakness of his treatment, i.e. proposing high numbers of species in the absence of providing a modern systematic revision.

Thus, it is currently difficult to understand the biology and systematics of the genus *Lavigeria*. For example, it has been proposed that viviparity in Lake Tanganyika gastropods in general and in *Lavigeria* in particular was a major factor in the causation of the radiation of species flocks and species richness, respectively (Cohen and Johnston 1987, Michel 1994). This claim has been discussed and rejected by Glaubrecht (1996, 2001, see also Strong and Glaubrecht 2002). First, most thalassoid gastropods are actually not viviparous but oviparous, and second, those genera that are viviparous, other than *Lavigeria*, in particular *Tanganyicia* Crosse, 1881 and *Tiphobia* Smith 1880, are monotypic. What is special about *Lavigeria*? This taxon has a unique morphological diversity, tempting Todd and Michel (2001) to, "delimit working species-concepts using these shell characters, independent of geographical considerations to prevent occurrence information biasing our identifications and then assign the nominal species to our concepts." Apart from the authors' unconventional idea of what a "concept" of a species is and how to "assign" the latter to the former (see discussion above), this procedure resulted in their conclusion that their "systematic framework for the genus currently consists of over 30 species," and that "many more species remain to be discovered as sampling improves" (Todd and Michel 2001: 355). The question remains unanswered what natural (spe-

ciation) mechanism causes this enormous species flock to evolve and whether there is any ecological and/or geographical correlation indicative of, for example, habitat specificity and fragmentation and/or intralacustrine allopatry. In contrast to the procedure chosen by these authors, who do not want to be "biased" by information on occurrences, evaluating the actually morphological disparity and purported taxonomic diversity in *Lavigeria* within a microgeographical framework that includes the ecological context would be a most promising research program to address the species question.

## Case 2: The species question in North American Pleuroceridae

The Pleuroceridae has long been recognized "as one of the most difficult families of American mollusks," (Pilsbry and Rhoads, 1896: 495). For more than a century, high degrees of shell variation caused authors to describe a plethora of species and subspecies. The bewildering variety of shell phenotypes, interpreted as the result of an extensive endemic radiation particularly in streams and rivers of the southeastern USA posed tremendous problems to the systematics of this group. Accordingly, Dillon (1984: 70) noted that "pleurocerid taxonomy is currently in a confused state."

The outstanding (and still most comprehensive) systematic monograph of this family by George W. Tryon (1873) listed a total of 464 species for North America. In his treatment of the genus *Elimia* H. and A. Adams, 1854 (= *Goniobasis* Lea, 1862) alone, Tryon recognized 255 species. He later clearly saw that a reduction of pleurocerid species must be made, coming to the belief in 1888 that "there were not more than a tenth as many good species as names" (see Pilsbry and Rhoads 1896: 496). In the introduction to his monograph, Tryon (1873: li) had remarked concerning the morphological variation found in pleurocerids: "We thus find that no one character (with very few exceptions) can be relied on in species discrimination, but rather a combination of characters, with a general idea of the necessary allowance for variation pervading other species of the same general type, or contiguous locality."

Like many of his contemporaries, Tryon was aware of the species problem but not of the solution to it. In adding to his monograph the correspondence with another contemporary malacologist, James Lewis, Tryon gave some insight into the debate. For example, in discussing the most variable species from the creeks in Tennessee with "a perfect series of differentiations of carinated apices," Lewis (cited in Tryon 1873: 424-426) remarked that "one cannot tell where to assign limits. Limits are apparently obliterated and species have no existence. We are very largely at the mercy of opinion, some of which, no doubt, are but the reflex of the idiosyncrasies of the persons with whom they originate."



What Lewis very aptly called the “key to the origin of many of our species” provides an explanation for the typological species-making in freshwater gastropods. Because it was common practice of local collectors to send only single shells for identifications to experts of the group, it appears as no “wonder then, that the descriptive naturalist should unwittingly fall into a very natural mistake and describe these shells as new species” (see Tryon 1873: 426)

Pilsbry (*in* Pilsbry and Rhoads 1896: 496) was aware that the same species often occurs in some localities with the shell sculptured throughout, in others with sculpture only on the upper portion, and in still other localities only with the characteristic sculpture on the earlier whorls. Anticipating a research program finally taken up much later, he concluded that “these shells must be collected and studied by river-systems.” Goodrich (1940, 1942), for example, studied members of the Pleuroceridae in the Ohio river system and the Atlantic coastal plain, compiling data for 81 species from these drainage complexes (leaving others unmentioned, however). Thus, he first tried to sort out named shells from real biological entities and to clarify some of the confusion over the various names erected for this over-described family of aquatic snails.

In his compilation of North American freshwater snails, Burch (1982) provided the most and only recent overview, listing a total of 212 pleurocerid taxa (including subspecies and “morphs”), of which 152 were attributed species status. For the diverse and morphologically disparate genus *Elimia* alone he reduced the number given by Tryon (1873) by two-thirds, recognizing 83 species. Although it is generally realized now that there are problems with the delineation of species based solely on shell morphology in snails that exhibit clinal variation, Burch’s compilation still provides the only attempt so far to comprehensively treat the entire group. Nevertheless, any attempt to revise the Pleuroceridae and provide a formal systematic monograph is lacking, probably due to the enormous problems caused by the chaotic taxonomy resulting from former typological approaches.

Several studies comparing the amount of phenotypic and genotypic variability in pleurocerid species from various river drainages, using measurements of genetic divergence/similarity based on allozymes (for example Chambers 1980, Dillon and Davis 1980, Dillon 1984, Dillon and Lydeard 1998) or mitochondrial sequence data (Lydeard *et al.* 1997, 1998, Holznagel and Lydeard 2000, Mihalcik and Thompson 2002), reveal conflicting evidence as to the morphological and genetic/molecular concordance within and among species and genera of pleurocerids. From the results on pleurocerids it was concluded, (1) that morphological variability is correlated with environmental differences, (2) that species

identification using shell morphology alone is often unreliable, (3) that because intrapopulation genetic variation is low and interpopulation divergence is high gene flow even among conspecific populations connected through water can be quite low, and (4) that there are different views of species relationships and taxonomy based on electrophoretic studies and molecular genetic data compared to previous work based on shell morphology. For example, for taxa of the *Elimia* (= *Goniobasis*) *floridensis* (Reeve, 1860) species complex in Florida, Chambers (1980) reported that the divergence in shell sculpture was accompanied by little or no genetic divergence, which has been greatly facilitated by the low frequency of dispersal between drainage systems. Given that the geographic distribution of these freshwater gastropods are subdivided by the discontinuities of their habitat, Chambers (1980) favored an allopatric model of speciation when concluding that geographic barriers between populations have probably played a major role in promoting the complex pattern of speciation observed in the evolution of Pleuroceridae.

Studying species of *Elimia* occurring from Virginia to Georgia, Dillon (1984) emphasized a strong correlate of geographic distance with genetic divergence between populations. Thus, although the range of a species is fragmented into a large number of isolated populations separated from one another by mountains between drainages and by stretches of large, apparently uninhabited river (Dillon and Reed 2002), genetic cohesion is maintained even with negligible gene flow. Geographically isolated populations not sharing alleles at many studied allozyme loci did not demonstrate reproductive isolation, as Dillon and Lydeard (1998) noted. Similarly, in a study of the species of the pleurocerid genus *Leptoxis* inhabiting the Mobile River basin of Alabama, Dillon and Lydeard (1998) found some of their data to be more consistent with a hypothesis of geographic isolation rather than reproductive isolation (see also Dillon and Reed 2002). Nevertheless, they strongly advocate special attention and conservation status for those pleurocerid populations to which species status would be attributable on the basis of high genetic divergence.

With respect to the number of species as well as how and where to delineate species-level taxa in Pleuroceridae, many contradicting arguments have been put forward, at least in part based on the considerable mismatch between morphologically distinguishable taxa and those found either by electrophoretic studies or by molecular genetic analysis (mtDNA). For example, stating that certain shell characters (for example, sculpture) can give a misleading view of interspecific boundaries and relationships, Chambers (1990) recognized only four species of *Elimia* in Florida river drainages, namely *Elimia floridensis* (Reeve, 1860), *Elimia dickinsoni* (Reeve, 1860), *Elimia* sp. 1, and *Elimia* sp. 2.

*soni* (Clench and Turner, 1956), *Elimia boykiniana* (Lea, 1840), and *Elimia curvicastrata* (Reeve, 1861), where earlier treatments had considered 10 species. In contrast, Thompson and Mihalcik (2002) and Mihalcik and Thompson (2002) identified the previously recognized *Elimia curvicastrata* from rivers in western Florida to Georgia, for which Chambers has listed 10 junior synonyms, as a complex of 14 morphologically distinct species, describing five new species and two new subspecies. These authors propose that because of convergence in adult shells, the juvenile shells are of primary importance in distinguishing species. In their parallel molecular analysis they found five distinct species clusters that correlate geographically to different river drainages. Earlier, Thompson (2000) described, based on morphological evidence only, four additional species of *Elimia* from the Coosa River drainage in Alabama.

A similar association of clades in a molecular phylogeny with drainage basin rather than with traditional morphological groupings of the currently recognized taxa was found in studies of the pleurocerids from the Mobile Basin (Sides 2002). Minton (2002) found, in a cladistic analysis of the genus *Lithasia* from the Cumberland, Ohio, and Tennessee River drainages that morphological characters (shells and radulae) alone neither recover currently or historically recognized groups at the species level nor do they match with those taxa delineated based on molecular phylogenetic analysis (see also Lydeard *et al.* 1997). In addition, Minton and Savarese (2002) found evidence for the existence of an undescribed phylogenetic species in the Harpeth River, Tennessee, this time explicitly applying the concept of phylogenetic species in their study.

Based on studies on genetic variation at allozyme loci among populations of two species of *Elimia*, *Elimia proxima* (Say, 1825) and *Elimia catenaria* (Say, 1822) from the Atlantic drainages of the Carolinas, Dillon and Reed (2002) called into question the species' identifications and status of some nominal species and subspecies and their relationship in neighboring Atlantic drainages. For example, they suggested that *E. catenaria* might occur also in Georgia (and maybe even further south), instead of applying different names to populations with slightly distinct morphological (shell) characters whenever found in different drainages of an adjacent state.

Although the century-old suggestion to study pleurocerid systematics by river systems instead of typological naming of individual shells has finally been taken, a general disagreement on how to apply species concepts to these highly polymorphic freshwater gastropods in light of new biochemical methods has not yet greatly improved the situation. Currently, the systematics of Pleuroceridae are constrained between the Scylla of a relatively wide approach of

molecular phylogenetics that chiefly resolves intergeneric relationships in an effort to understand the evolution of the entire family (Holznagel and Lydeard 2000) and the Charybdis of a narrow focus on populations within individual rivers or drainages and a restriction to only few species-level taxa (Dillon 1984, Lydeard *et al.* 1997, Dillon and Reed 2002, Minton 2002, Sides 2002). Taking the geographical context into consideration on a larger scale, such as comparing congeneric taxa like *Elimia* or *Leptoxis* across their entire distributional ranges and all inhabited drainage systems, in concert with a cladistic analysis of morphological and molecular data would greatly enhance our understanding of the nature of species in these North American gastropods.

## CONCLUSION

Nature, in some respects, comes to us as continua, not as discrete objects with clear boundaries . . . But since nature has built a continuum, we must encounter ambiguity at the center. Some cases will be impossible to call—as a property of nature, not an imperfection of knowledge (Gould 1985)

## Species as dynamic entities

Species are, and therefore should be conceived of as, dynamic entities that need to be placed in historical as well as geographic contexts. Biological discontinuities such as reproductive isolation by which the species are characterized in nature should be utilized to define them. Among the plethora of species concepts suggested in the past, the BSC and the PSC(s) confront us with the twin dangers of either "overlumping" obviously distinct specific variation (on phenotypic and on genetic grounds) via strict application of the BSC, or oversubdividing biodiversity on lowest taxonomic levels. Because things in nature that seem distinct may represent the extremes of a continuum, I have emphasized (1) the historic dimension of the species debate and (2) the horizontal dimensionality of the species concept, that is the geographical factor in the discussion on the nature of species. In order to recognize biological species as evolutionary and ecological units we need to combine data on geographic variation with information on dispersal and environmental history (i.e. the biogeographical patterns). To this purpose, the BSC provides the only non-arbitrary criterion available, namely the presence or absence of interbreeding between two populations coexisting temporally and spatially. In contrast, the PSC determines species status based on the subjective and arbitrary criterion of diagnosability (that is, species as the smallest diagnosable units).

Biologists should be more aware and, consequently, explicit in applying different conceptual approaches to the species problem. If not using the concept of a biological species



as reproductive community but focussing on diagnosability only (either at the morphological or molecular level), authors should explain their line of argument as to their perception of species in nature. For the most interesting and spectacular case studies of enlarged species diversity as recently discovered, for example, in limnic hydropbiids in North America and Australia, or some thalassoid molluscs in ancient lakes such as Lake Tanganyika and the central lakes on Sulawesi, the taxonomic descriptions of the many new taxa should be supplemented by addressing the general problems of species discrimination with a non-essentialistic species concept. Within the framework of evolutionary knowledge and population thinking the discussion and analysis of speciation in those cases would certainly enrich the century-old debate on the origin of species diversity.

There are many approaches in malacology today to overcome the purely descriptive tradition that resulted from the often uncritical multiplication of taxa names during the typological times of the 19<sup>th</sup> century. Modern taxonomy is increasingly aware of the uniqueness of individuals on the one hand and the wide range of variation within any population of individuals on the other hand. While malacology is often too narrowly focussed on accumulating data, other disciplines, such as ornithology, led the way in testing general evolutionary theories, including the predictions from species concepts and speciation hypotheses. What is needed is the integrated synthesis between the malacologist compiling observations from the field and laboratory and the malacologist evaluating theories within the framework of historical achievements.

Rather than a lack of definitions, the real neglect is the absence of a clear statement of why and on which grounds decisions on species status have been made. Too often in systematic revisions and other taxonomic accounts, any reference to the species concept is either lacking or the definitions given and/or used are unconventional, incorrect, or misleading. As long as this situation continues, the progress in systematic science is hampered as much as during Darwin's days, when "different naturalists made different decisions on different grounds, with the result that the decisions—and the entities dealt with—certainly did appear purely arbitrary" (Kottler 1978: 296). In this context, and in turning around the traditional tendency to look and describe "specific" differences, we should start with a single species as null hypothesis. In examining any set of morphological and genetic data we should only accept the more complex hypothesis of two or more species if a better fit with the data available necessitates this.

### Towards a phylogeographical synthesis

There is a long research tradition in zoology of geographical variation and the characterization of geographic varieties. We need to re-vitalize this tradition and at the

same time employ newly available molecular and other techniques, as exemplified recently in phylogeography. This field of study is concerned with the principles and processes governing the geographical distribution of genealogical lineages, especially those within and among closely related species (for review see Avise 2000a). A primary requirement of the expansion of empirical studies of comparative phylogeography is the acquisition of biogeographic information on a regional scale. In many cases in invertebrate zoology, however, those basic biogeographic data are not available, thus hampering the integration of genealogical data. Concerning the question of how to delineate species, we are not suffering from a lack of definitions, but rather from incomplete biological information. The recent molecular revolution of phylogenetics with the now widely-used methods of PCR and sequencing has provided powerful tools for species-level studies based on the reconstruction of past events and geographic modes. For example, within limnic molluscs with confusing taxonomy and poorly understood biogeography, this is most recently exemplified by the mudsnail species of the hydrobiid genus *Hydrobia* (Wilke *et al.* 2000) and by the limnic bivalves of the genus *Corbicula* (Pfenniger *et al.* 2002).

There is a great need for the integration of more data, not only on morphological and molecular variation but also on geographic distribution. The fact that the range of intra-specific variation over a given region is often insufficiently known renders any evaluation of gene flow among populations hazardous. The importance of knowing the structure of the population genetics of a species or species complex as a prerequisite for determining the genetic units has been illustrated recently for the epidemiologically important vector of malaria *Anopheles gambiae* s. str. (della Torre *et al.* 2002) and for some snails that are vectors for schistosomiasis (reviewed recently by Blair *et al.* 2001).

### Future challenges

Any in-depth debate of the species question in malacology faces two major challenges: first, to get more of the relevant data for as many taxa and case studies as possible and second, because natural processes are constrained by a three-dimensional space, to make inferences in the appropriate spatial and temporal context. To gain the data for these inferences, the various stages of differentiation, particularly in contact zones and nearby areas, should be focussed on, and molecular and morphological variation tested in allopatry, parapatry, and sympatry, with the aim of attributing the status of allospecies, paraspecies, or semispecies to local populations (Fig. 1). Attempts to make these inferences are led by the conviction of Stebbins (1969), albeit in another context, that "the best system for any group is one synthesized from data of all kind." Scrutinizing our ideas on the nature of species thus demands the integration of mor-

phology (from diagnostic biometry to anatomy and histology), molecular genetics, and biogeographical analyses supplemented by data from ecology, ethology, and other sources. Avise (2000a, 2000b) suggested that wedding the better elements of the traditional BSC and PSC will eventually produce a synthetic conceptual framework for species recognition. In this ongoing phylogeographic synthesis, population-demographic and population-genetic principles should be supplemented by historical geographic considerations. Instead of trying to find another species definition or concept, we should make use of the heuristic properties of the existing biological and phylogenetic ones.

A phylogeographic approach that combines the reproductive criterion of the BSC (such as barriers, isolates and geography) with the phylogenetic criterion of the PSC (namely historical and demographic aspects) will eventually lead to a most fruitful synthesis. The increasingly better and more detailed documentation of morphological and molecular genetic differentiation of molluscs in their spatiotemporal context will result in a taxonomically improved classification based on insights from biology and phylogeny. Freeing malacology from the typological naming of whatever was previously diagnosed as "species" will then truly become Leopold von Buch's legacy.

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